

La estructura de las redes mutualistas

Esquema conceptual de la charla

- Breve historia de los estudios de redes mutualistas
- Estructura de las redes de interacciones mutualistas
- Mecanismos responsables de los patrones observados en redes mutualistas

PATTERNS OF MUTUALISTIC INTERACTIONS IN POLLINATION AND SEED DISPERSAL: CONNECTANCE, DEPENDENCE, ASYMMETRIES, AND COEVOLUTION

PEDRO JORDANO

Unidad de Ecología y Etología, Estación Biológica de Doñana, 41013 Sevilla, Spain

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Animals are the main transfer agents during the two dispersive phases of reproductive cycles in higher plants: pollination of flowers and seed delivery to germination sites. The relationship is mutually beneficial, since animals use the variety of resources provided by plants around the reproductive structures (floral parts, nectar, fragrances, fleshy pulp, etc.). These mutual benefits have been a major factor in the evolution of angiosperms (Mulcahy 1979; Tiffney 1984), insects (Strong et al. 1984), and several groups of vertebrates (Snow 1971, 1981; Stiles 1981; Heithaus 1982; Marshall 1983).

Consideration of the ways plant and animal mutualists interact is fundamental for understanding coevolution as a reciprocal evolutionary change. However, coevolutionary change is basically a diffuse process involving sets of species, and pairwise coevolution (Janzen 1980) is rare in most plant-animal mutualisms

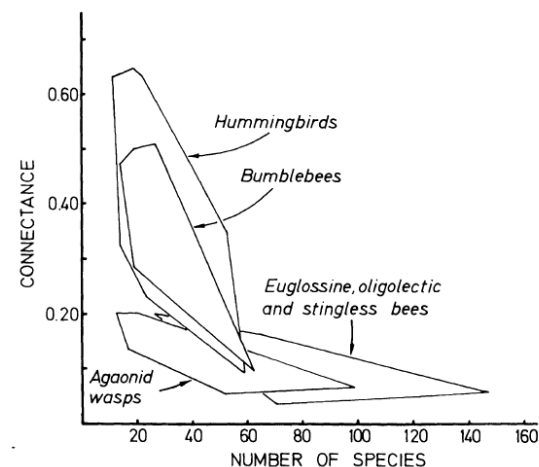
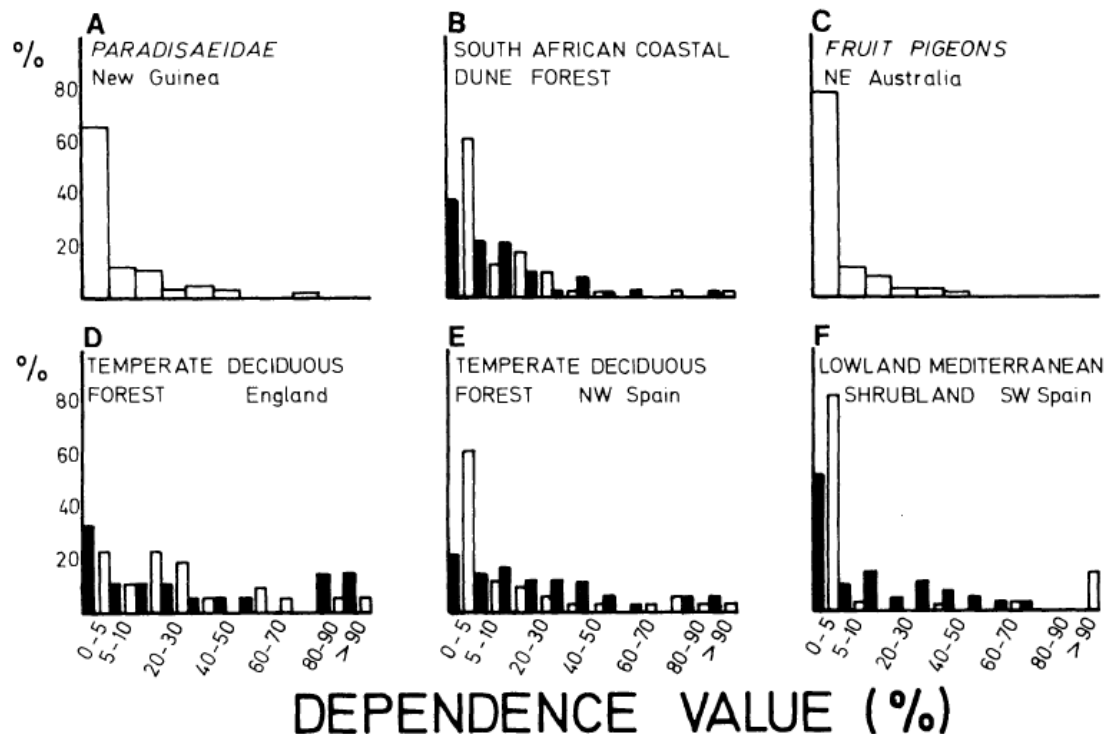


FIG. 2.—Connectance decreases with increasing species richness in plant-pollinator mutualisms. Differences in connectance values for different types of pollinators suggest specific modes of interaction (polygons include the range of values for different groups; see table 1).



GENERALIZATION IN POLLINATION SYSTEMS, AND WHY IT MATTERS¹

Nickolas M. Waser,^{2,3} Lars Chittka,^{4,5} Mary V. Price,^{2,3}
Neal M. Williams,⁴ and Jeff Ollerton⁶

Abstract

One view of pollination systems is that they tend toward specialization. This view is implicit in many discussions of angiosperm evolution and plant–pollinator coevolution and in the long-standing concept of “pollination syndromes.” But actual pollination systems often are more generalized and dynamic than these traditions might suggest. To illustrate the range of specialization and generalization in pollinators’ use of plants and vice versa, we draw on studies of two floras in the United States, and of members of several plant families and solitary bee genera. We also summarize a recent study of one local flora which suggests that, although the colors of flowers are aggregated in “phenotype space,” there is no strong association with pollinator types as pollination syndromes would predict. That moderate to substantial generalization often occurs is not surprising on theoretical

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² Department of Biology, University of California, Riverside, California 92521 USA.

³ Rocky Mountain Biological Laboratory, P.O. Box 519, Crested Butte, Colorado 81224 USA.

⁴ Department of Ecology and Evolution, State University of New York, Stony Brook, New York 11794 USA.

⁵ Institut für Neurobiologie, Freie Universität Berlin, Königin-Luise-Strasse 28–30, 14195 Berlin, Germany.

⁶ School of Environmental Sciences, Nene College, Park Campus, Moulton Park, Northampton NN2 7AL, United Kingdom.

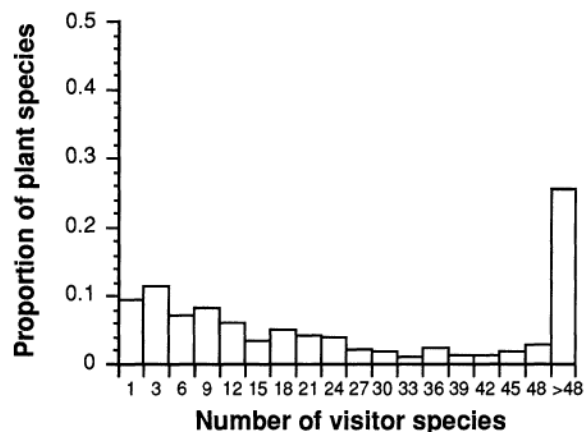


FIG. 1. Pollinator affinities in the Carlinville, Illinois (USA) flora, from records in Robertson (1928). Frequency distribution of the proportions of 375 native plant species receiving pollination visits from different numbers of animal species.

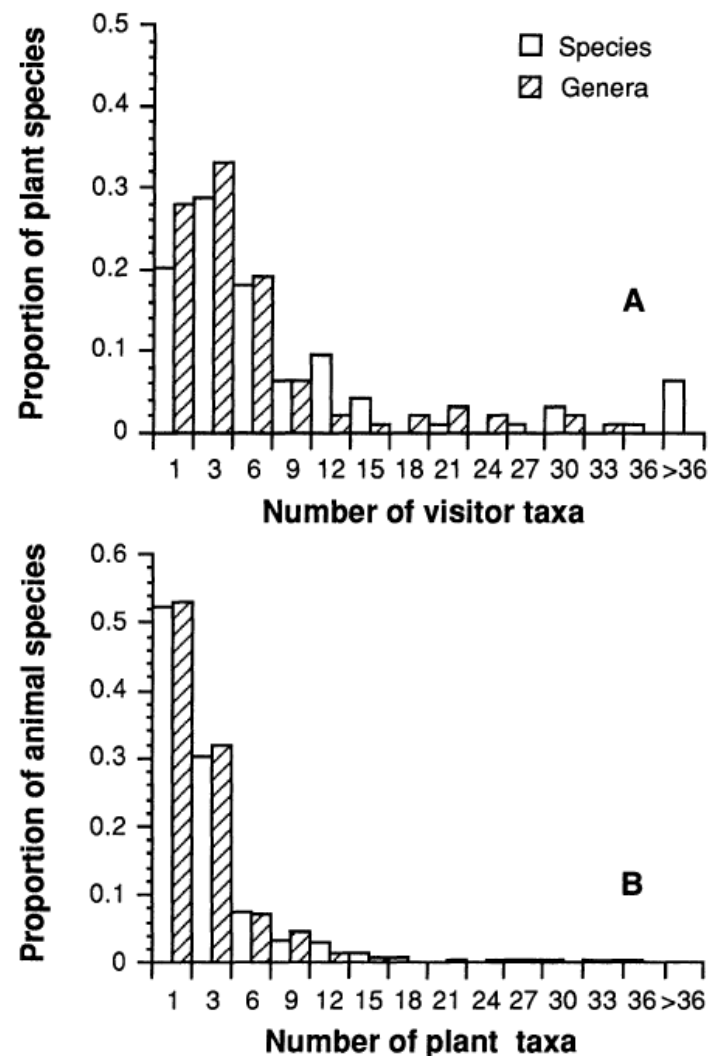


FIG. 2. Plant and pollinator records from Pike's Peak, Colorado (USA), from records in Clements and Long (1923). (A) Frequency distribution of the proportions of 94 native plant species receiving visits from different numbers of animal species and genera. (B) Frequency distribution of the proportions of 268 native animal species visiting different numbers of plant species and genera.

The structure of a plant–pollinator food web

Jane Memmott

School of Biological Sciences,
University of Bristol, Woodland
Road, Bristol, BS8 1UG, UK.
E-mail:
Jane.Memmott@bris.ac.uk

Abstract

The pollination biology literature is dominated by examples of specialization between plants and their pollinators. However, a recent review shows that it is generalization that prevails in the field, with most plants having a number of pollinators and most pollinators visiting a number of plants. Consequently, the vast majority of plant–pollinator interactions are embedded in a complex web of plant–pollinator interactions. These plant–pollinator webs can be studied in the manner of conventional food webs and the aim of this paper is to illustrate how contemporary methods of web construction and analysis can be applied to plant–pollinator communities.

Keywords

Food web, generalization, pollination, pollinators, specialization

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65, 339–347

Asymmetries, compartments and null interactions in an Amazonian ant–plant community

CARLOS ROBERTO FONSECA* and GISELENE GANADE†

*Animal Behaviour Research Group, Department of Zoology, South Parks Road, Oxford, OX1 3PS, UK; and,

†NERC Centre for Population Biology and Department of Biology, Imperial College at Silwood Park, Ascot, Berks SL5 7PY, UK

Summary

1. In the tropics, many plants offer housing and food for their specialized ant partners which, in return, offer benefit in the form of defence and/or nutrients, thus forming mutualistic bonds. Such ant–plants, also called myrmecophytes, occur together at a local scale, generating community patterns of mutualistic ant–plant associations. Here,

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GEOGRAPHIC PATTERNS IN PLANT–POLLINATOR MUTUALISTIC NETWORKS

JENS M. OLESEN^{1,3} AND PEDRO JORDANO²

¹Department of Ecology and Genetics, University of Aarhus, Ny Munkegade Block 540, DK-8000 Aarhus, Denmark

²Estación Biológica de Doñana, CSIC, Pab. Perú, Avda. M. Luisa S/N, E-41013 Sevilla, Spain

Abstract. Recent reviews of plant–pollinator mutualistic networks showed that generalization is a common pattern in this type of interaction. Here we examine the ecological correlates of generalization patterns in plant–pollinator networks, especially how interaction patterns covary with latitude, elevation, and insularity. We review the few published analyses of whole networks and include unpublished material, analyzing 29 complete plant–pollinator networks that encompass arctic, alpine, temperate, Mediterranean, and subtropical–tropical areas. The number of interactions observed (I) was a linear function of network size (M) the maximum number of interactions: $\ln I = 0.575 + 0.61 \ln M$; $R^2 = 0.946$. The connectance (C), the fraction of observed interactions relative to the total possible, decreased exponentially with species richness, the sum of animal and plant species in each community ($A + P$): $C = 13.83 \exp[-0.003(A + P)]$. After controlling for species richness, the residual connectance was significantly lower in highland (>1500 m elevation) than in lowland networks and differed marginally among biogeographic regions, with both alpine and trop-



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Integration of alien plants into a native flower–pollinator visitation web

Jane Memmott¹* and Nickolas M. Waser²

¹School of Biological Sciences, University of Bristol, Bristol BS8 1UG, UK

²Department of Biology, University of California, Riverside, CA 92521, USA

Introduced alien species influence many ecosystem services, including pollination of plants by animals. We extend the scope of recent 'single species' studies by analysing how alien plant species integrate themselves into a native flower visitation web. Historical records for a community in central USA show that 456 plant species received visits from 1429 insect and 1 hummingbird species, yielding 15 265 unique interactions. Aliens comprised 12.3% of all plant species, whereas only a few insects were alien. On average, the flowers of alien plants were visited by significantly fewer animal species than those of native plants. Most of these visitors were generalists, visiting many other plant species. The web of interactions between flowers and visitors was less richly connected for alien plants than for natives; nonetheless, aliens were well integrated into the native web. Because most visitors appear to be pollinators, this integration implies possible competitive and facilitative interactions between native and alien plants, mediated through

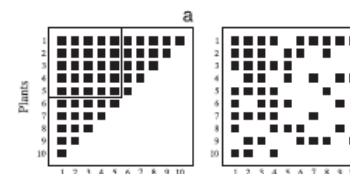
The nested assembly of plant–animal mutualistic networks

Jordi Bascompte^{1†}, Pedro Jordano², Carlos J. Melián¹, and Jens M. Olesen³

¹Integrative Ecology Group, Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, Apartado 1056, E-41080 Sevilla, Spain; and
²Department of Ecology and Genetics, University of Aarhus, Ny Munkegade, Building 540, DK-8000 Aarhus, Denmark

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Most studies of plant–animal mutualisms involve a small number of species. There is almost no information on the structural organization of species-rich mutualistic networks despite its potential importance for the maintenance of diversity. Here we analyze 52 mutualistic networks and show that they are highly nested; that is, the more specialist species interact only with proper subsets of those species interacting with the more generalists. This assembly pattern generates highly asymmetrical interactions and organizes the community cohesively around a central core of interactions. Thus, mutualistic networks are neither randomly assembled nor organized in compartments arising from tight, parallel specializa-



Ecology Letters, (2003) 6: 69–81

REPORT

Invariant properties in coevolutionary networks of plant–animal interactions

Abstract

Plant–animal mutualistic networks are interaction webs consisting of two sets of entities, plant and animal species, whose evolutionary dynamics are deeply influenced by the outcomes of the interactions, yielding a diverse array of coevolutionary processes. These networks are two-mode networks sharing many common properties with others such as food webs, social, and abiotic networks. Here we describe generalized patterns in the topology of 29 plant–pollinator and 24 plant–frugivore networks in natural communities. Scale-free properties have been described for a number of biological, social, and abiotic networks; in contrast, most of the plant–animal mutualistic networks (65.6%) show

Pedro Jordano^{1*}, Jordi Bascompte¹ and Jens M. Olesen²
¹Integrative Ecology Group, Estación Biológica de Doñana, CSIC, Apdo. 1056, E-41080 Sevilla, Spain
²Department of Ecology and Genetics, University of Aarhus, Ny Munkegade Block 540,

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NULL MODEL ANALYSES OF SPECIALIZATION IN PLANT–POLLINATOR INTERACTIONS

DIEGO P. VÁZQUEZ^{1,3} AND MARCELO A. AIZEN²

¹Department of Ecology and Evolutionary Biology, University of Tennessee, 569 Dabney Hall, Knoxville, Tennessee 37996-1610 USA

²Laboratorio Ecotono, C. R. U. B., Universidad Nacional del Comahue, Quintral 1250, (8400) Bariloche, Río Negro, Argentina

Abstract. Recent studies have suggested that plant–pollinator interactions may be less specialized than previously thought. We contrasted patterns of specialization observed in five plant–pollinator interaction webs with predictions based on null models. In the five data sets, the observed number of extreme specialists and extreme generalists was significantly higher than the null expectation. This pattern was mostly due to a positive correlation

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ASYMMETRIC SPECIALIZATION: A PERVERSIVE FEATURE OF PLANT–POLLINATOR INTERACTIONS

DIEGO P. VÁZQUEZ^{1,3} AND MARCELO A. AIZEN²

¹National Center for Ecological Analysis and Synthesis, University of California, 735 State Street, Suite 300, Santa Barbara, California 93101-3351 USA

²Laboratorio Ecotono, C.R.U.B., Universidad Nacional del Comahue, Quintral 1250, (8400) Bariloche, Río Negro, Argentina

Abstract. Although specialization in species interactions has usually been equated to reciprocal specialization, asymmetric specialization (i.e., a specialist interacting with a generalist) is also likely. Recent studies have suggested that asymmetric specialization in species interactions could be more common than previously thought. We contrasted patterns of asymmetric specialization observed in 18 plant–pollinator interaction webs with predictions based on null models. We found that asymmetric specialization is common in plant–pollinator interactions, and that its occurrence is more frequent than expected under a simple null model that assumed random interactions among species; furthermore, large assemblages with many pairs of interacting species tend to have more asymmetric interactions than smaller assemblages. A second null model, which incorporated a correlation between species frequency of interaction and degree of specialization observed in most data sets produced patterns that were generally closer to those present in the data. At least three kinds of explanations could account for the observed asymmetric specialization, including random interactions among individuals (rather than species), adaptive consequences of specialization, and artifacts, such as data aggregation and sampling biases. Future studies should be aimed at understanding the relative importance of each of these alternative

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- Estructura de las redes de interacciones mutualistas
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Pocas interacciones potenciales ocurren realmente (baja conectancia)

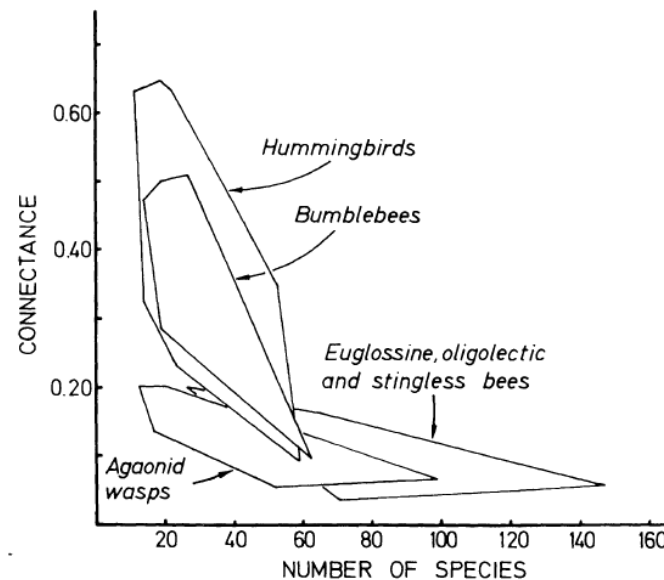


FIG. 2.—Connectance decreases with increasing species richness in plant-pollinator mutualisms. Differences in connectance values for different types of pollinators suggest specific modes of interaction (polygons include the range of values for different groups; see table 1).

Jordano P (1987) Am. Nat. 129: 657-677

Pocas especies con muchas interacciones, muchas con pocas

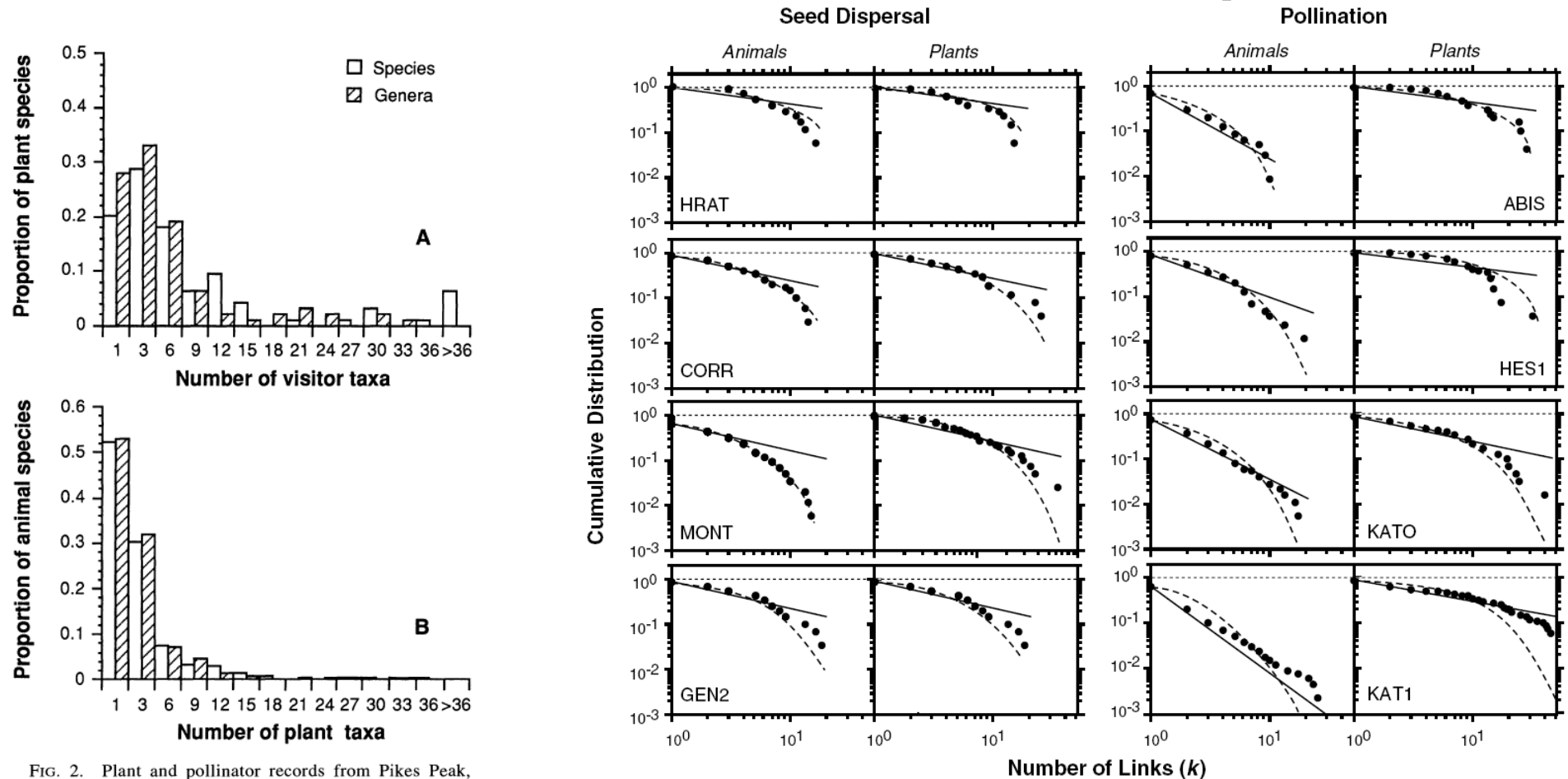


FIG. 2. Plant and pollinator records from Pikes Peak, Colorado (USA), from records in Clements and Long (1923). (A) Frequency distribution of the proportions of 94 native plant species receiving visits from different numbers of animal species and genera. (B) Frequency distribution of the proportions of 268 native animal species visiting different numbers of plant species and genera.

Figure 2 Cumulative distribution of connectivities (number of links per species, k , or degree) for different examples of the plant–animal interaction networks analysed (pollination and seed-dispersal mutualisms; Jordano 1987; Olesen & Jordano 2002). For these two-mode networks (see Fig. 1 for examples of the bipartite graphs) the distributions of links, $P(k)$, for the animal and plant species sets are given separately. Panels show the log-log plots of the cumulative distributions of species with 1, 2, 3, ..., k links (dots), power-law fits (solid lines) and truncated power-law fits (dotted lines). The distributions depart in most cases from the power-law beyond cut-off values, k_{∞} .

Muchas interacciones son débiles, pocas son fuertes

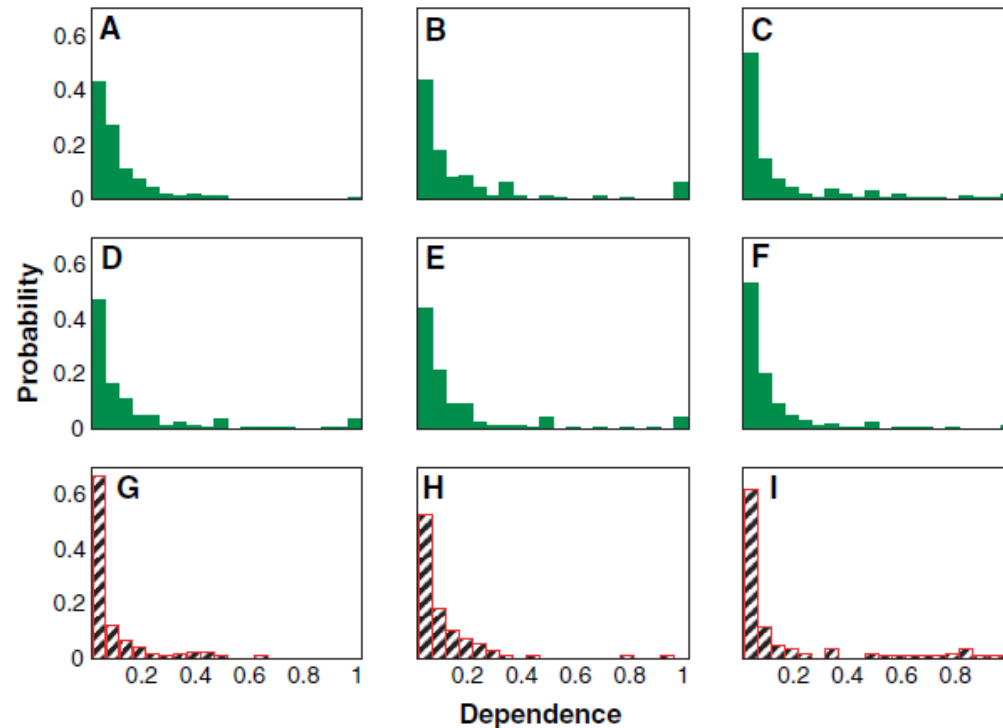


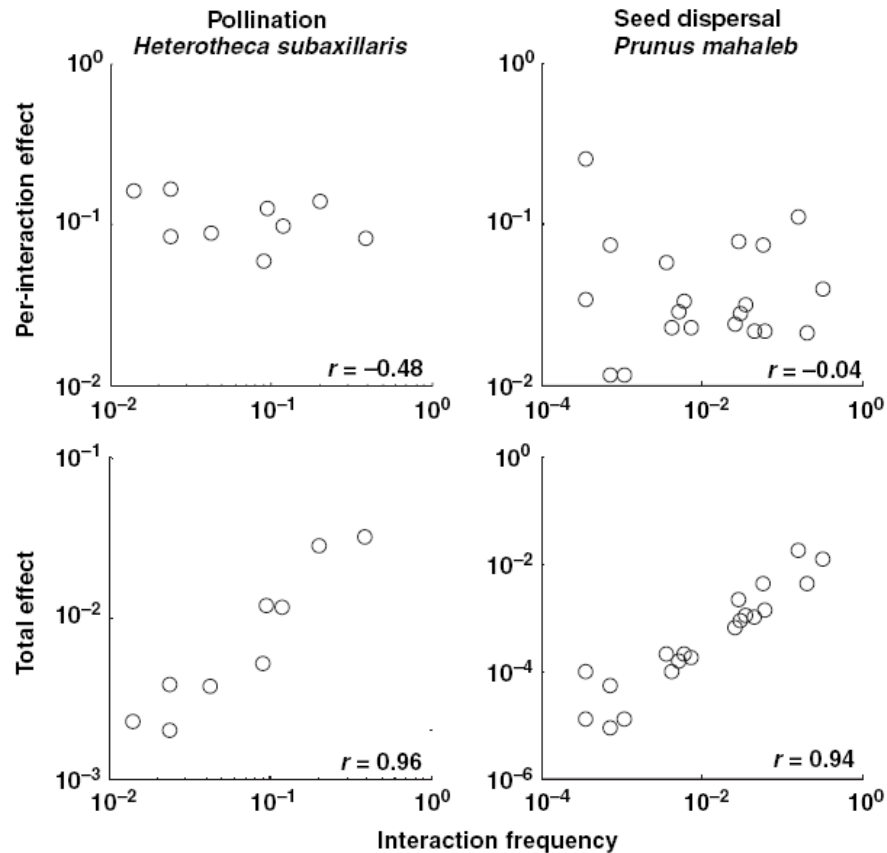
Fig. 2. Frequency distributions of dependence values within a mutualistic community. Green solid histograms (**A** to **F**) represent dependences of plants on pollinators, and red dashed histograms (**G** to **I**) represent dependences of seed dispersers on plants. See Database S1 for references and data sets.

Bascompte et al. (2006) Science 312: 431-433

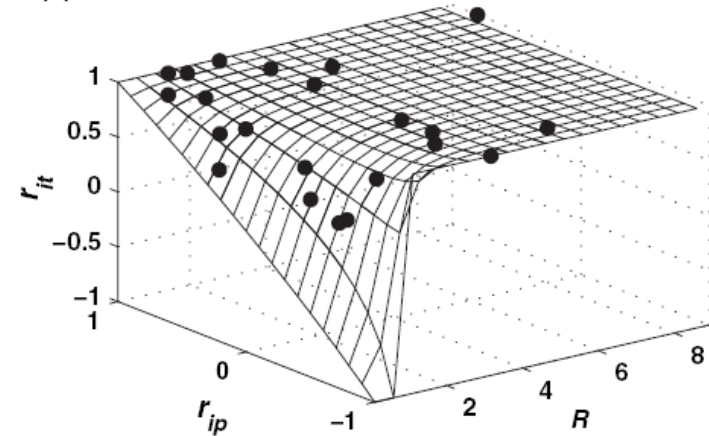
(Paréntesis: Cómo se mide la fuerza de la interacción)

- Impacto ecológico total (T) de una especie sobre otra: $A \rightarrow B$
- Dos componentes: frecuencia de interacción (I) y efecto por interacción (P): $T = IP$
- Medir P es difícil, y no hay datos para redes
- Estudios de redes mutualistas normalmente suponen que $T \approx I$, y que P puede despreciarse

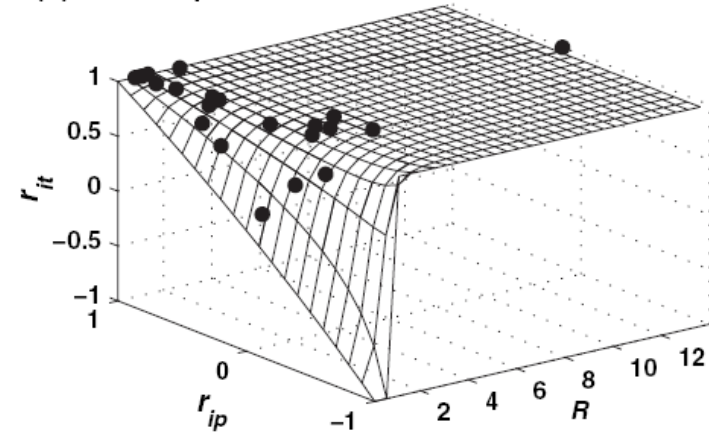
(Paréntesis: Cómo se mide la fuerza de la interacción)



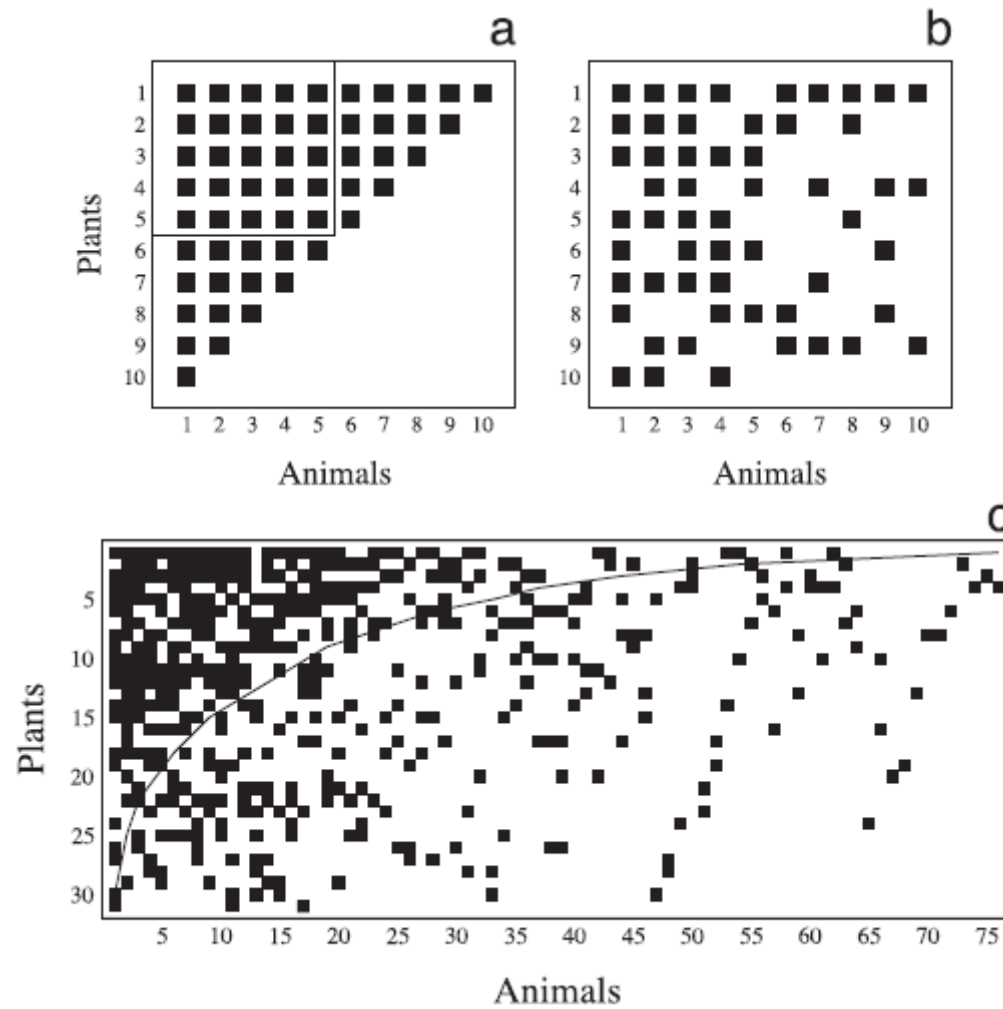
(a) Pollination



(b) Seed dispersal



Las redes mutualistas tienden a estar anidadas



La mayoría de las interacciones son asimétricas en términos de grado...

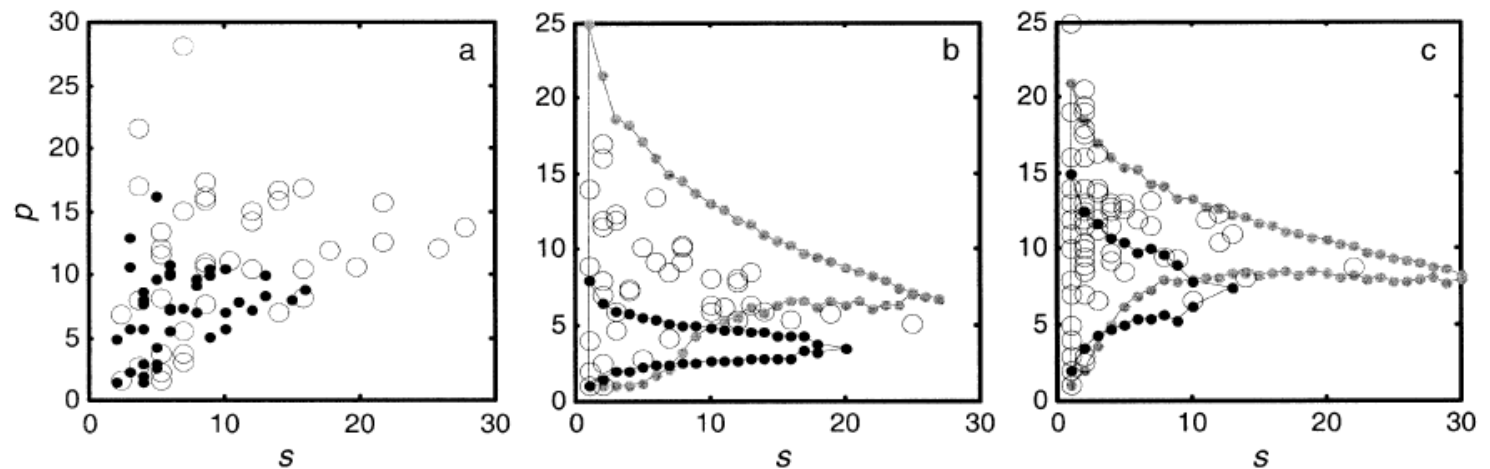
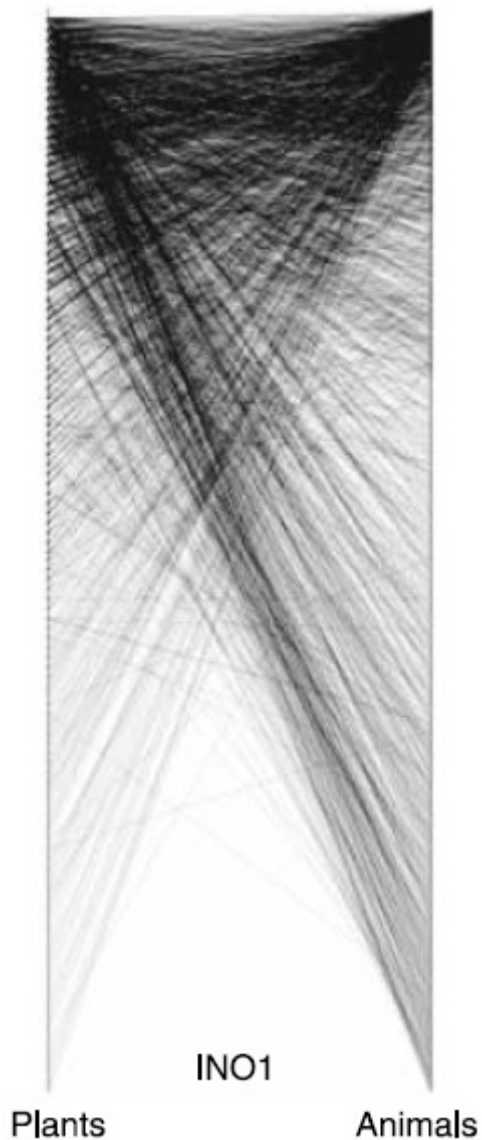


FIG. 1. Distribution of asymmetric specialization in plant–pollinator interaction networks. Plots show the average specialization of interaction partners (p) vs. the degree of specialization (s). (a) An example to illustrate the inability of the correlation coefficient to characterize asymmetric specialization. Heuristic data are shown for two communities with identical correlation coefficients ($r = 0.4265$), one with higher values of s and p (large open circles) than the other (black dots). Data for the Inouye and Pyke (1988) data set are shown for plants (b) and pollinators (c). Large open circles represent observed s - p values; black dots and line indicate the null space for model 1; gray dots and line indicate the null space for model 2. Notice that most extreme specialists (species with low values of s) do not have reciprocally specialized interaction partners (low values of p); a similar pattern was observed for all data sets (see Appendix B).

Vázquez & Aizen (2004) Ecology 85: 1251-1257

...y de fuerza de interacción

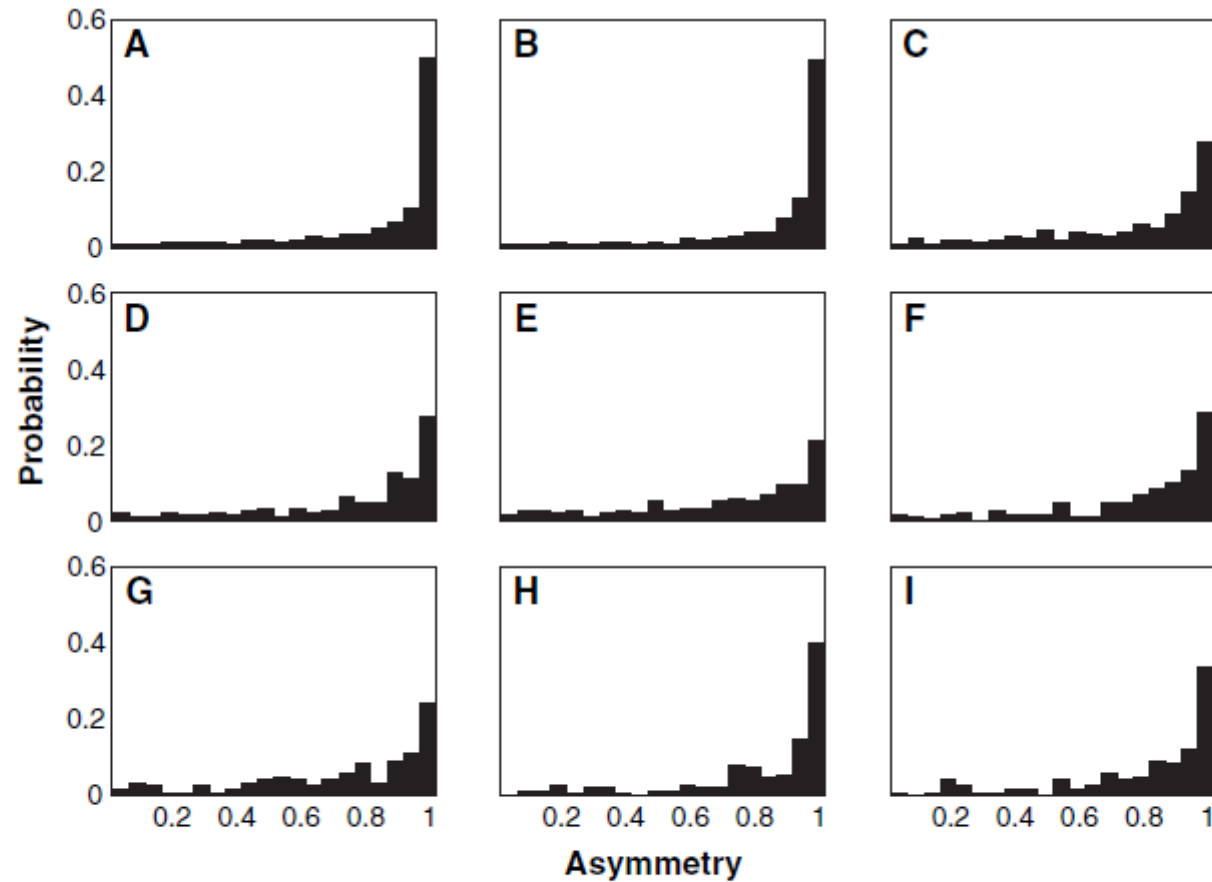
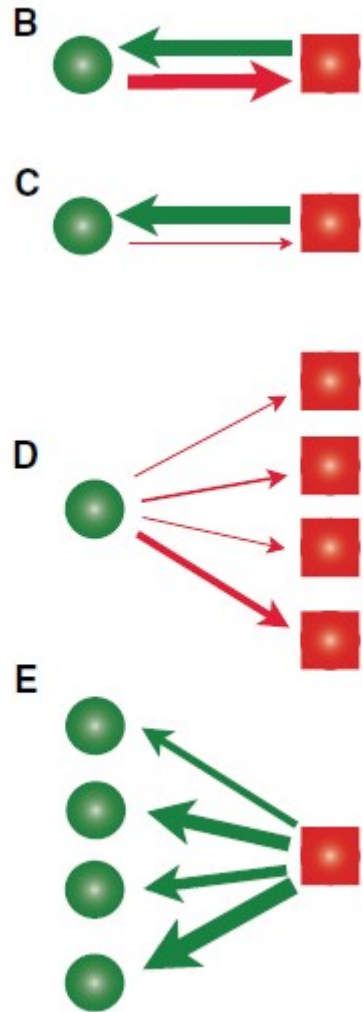
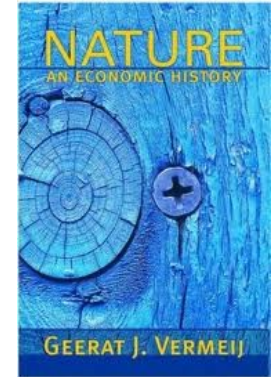


Fig. 3. Frequency distributions of asymmetry values of mutual dependences within a mutualistic community. (A to F) Plant-pollinator communities. (G to I) Plant seed-disperser communities. See Database S1 for references and data sets.

Bascompte et al. (2006) Science 312: 431-433

La asimetría como principio general

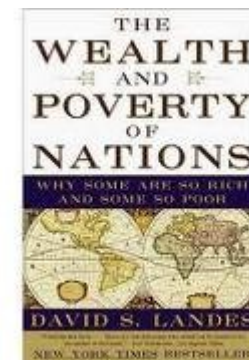
Uno de los principios más simples, y a la vez más trascendentes, en el ámbito de la economía es que, cuando dos entidades interactúan, casi siempre una gana más o pierde menos recursos que la otra. El resultado de la interacción es, en otras palabras, desigual con respecto al bien que está siendo intercambiado. [...] La mayoría de las interacciones económicas, tanto competitivas como cooperativas, desde organelas en una célula a biotas que interactúan a escalas evolutivas a través de barreras geográficas, están caracterizadas por la desigualdad. Del mismo modo, las sociedades y las instituciones humanas se caracterizan por una influencia desproporcionada y una distribución desigual de costos y beneficios, riesgos y recompensas, y niveles de rendimiento.



--G. Vermeij (2004) Nature: An Economic History. Princeton U. P.

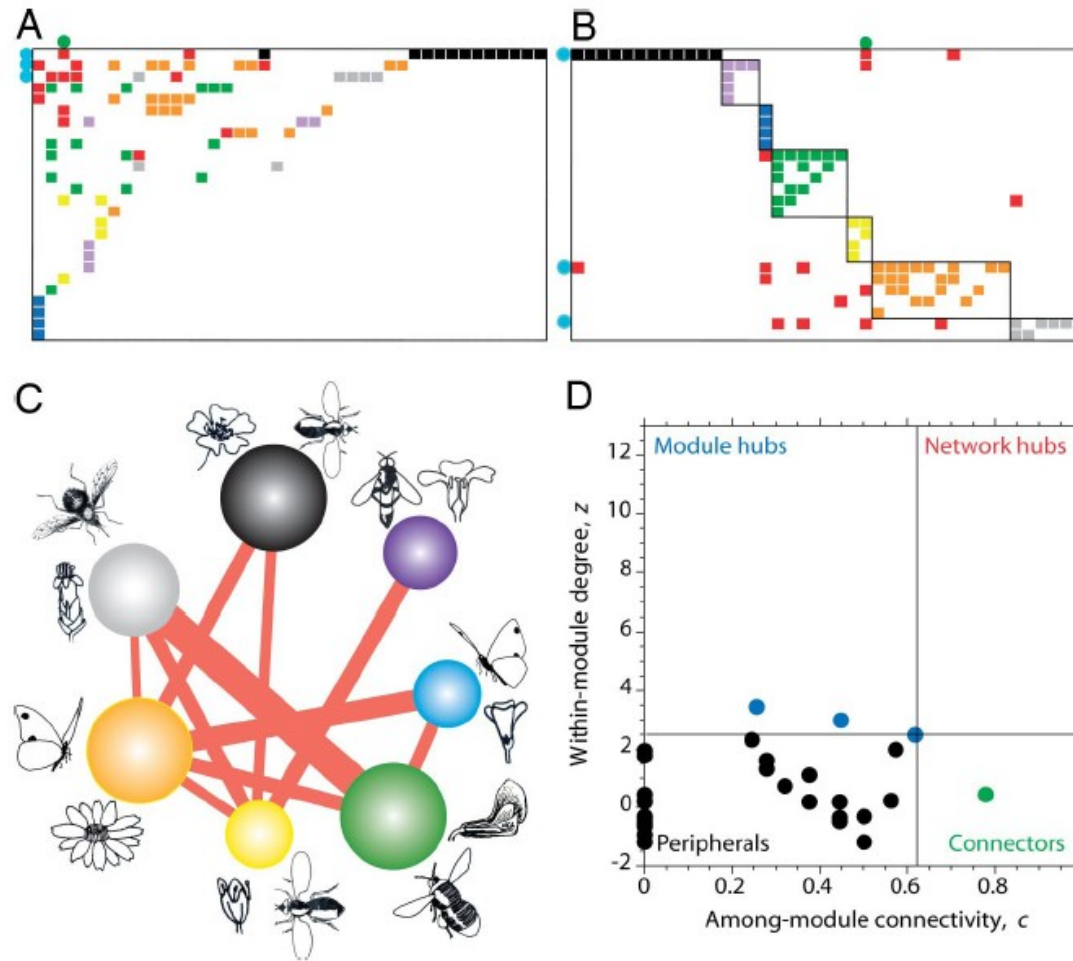
La asimetría como principio general

Propondría una ley de relaciones políticas y sociales, específicamente, que hay tres factores que no pueden coexistir: (1) una disparidad marcada en el poder; (2) el acceso privado a los instrumentos de poder; y (3) la igualdad entre grupos o naciones. Donde un grupo es lo suficientemente fuerte como para arrastrar a otro y beneficiarse por ello, lo hará. Aun si el estado se abstuviera de la agresión, las compañías y los individuos no esperarán autorización. Por el contrario, actuarán según sus propios intereses, arrastrando a otros, incluyendo al estado.



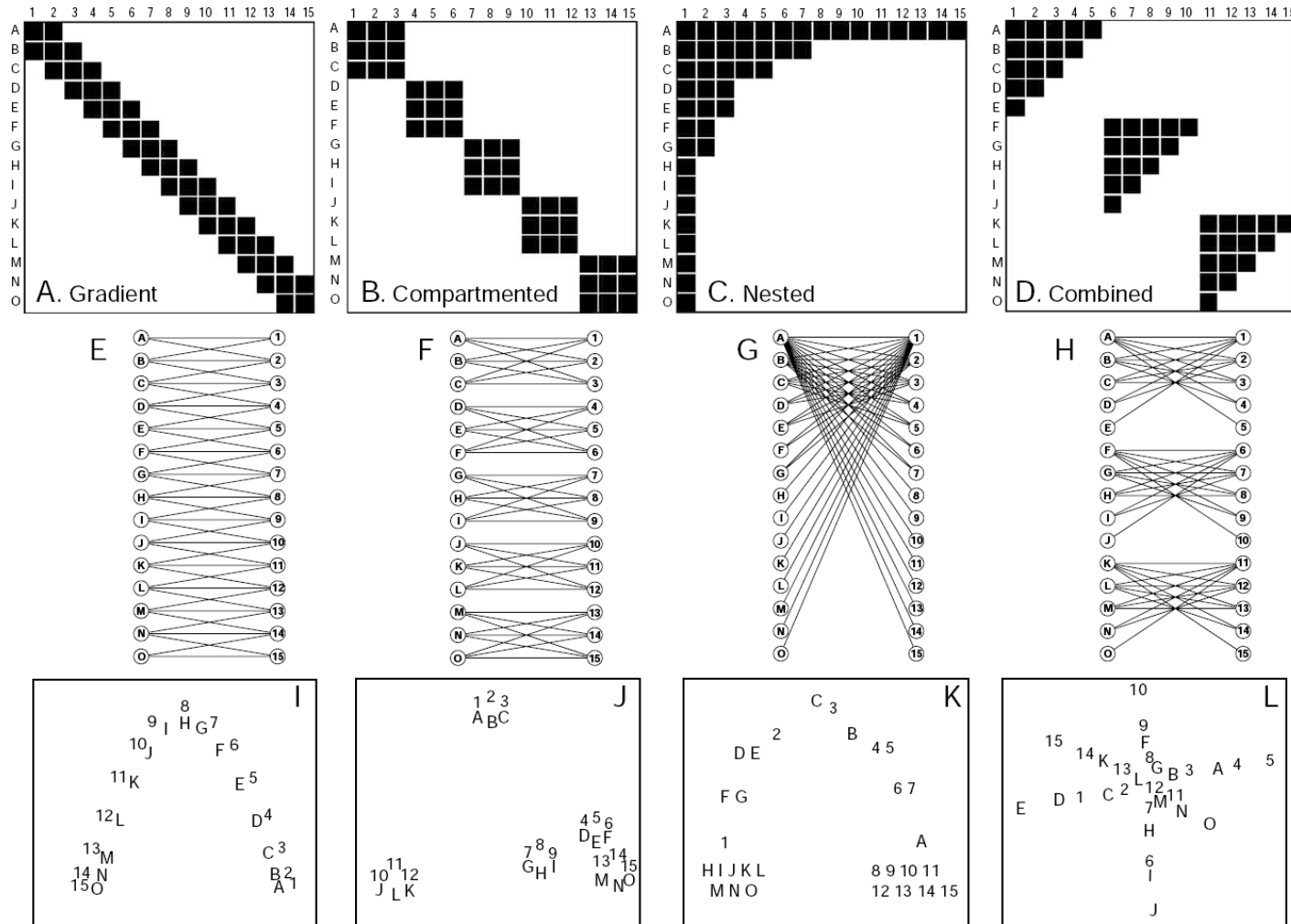
--D. S. Landes (1998) The Wealth and Poverty of Nations. Norton.

Las redes mutualistas tienden a estar compartimentalizadas



Olesen et al. (2007) PNAS 104: 19891-19896

Integrando patrones



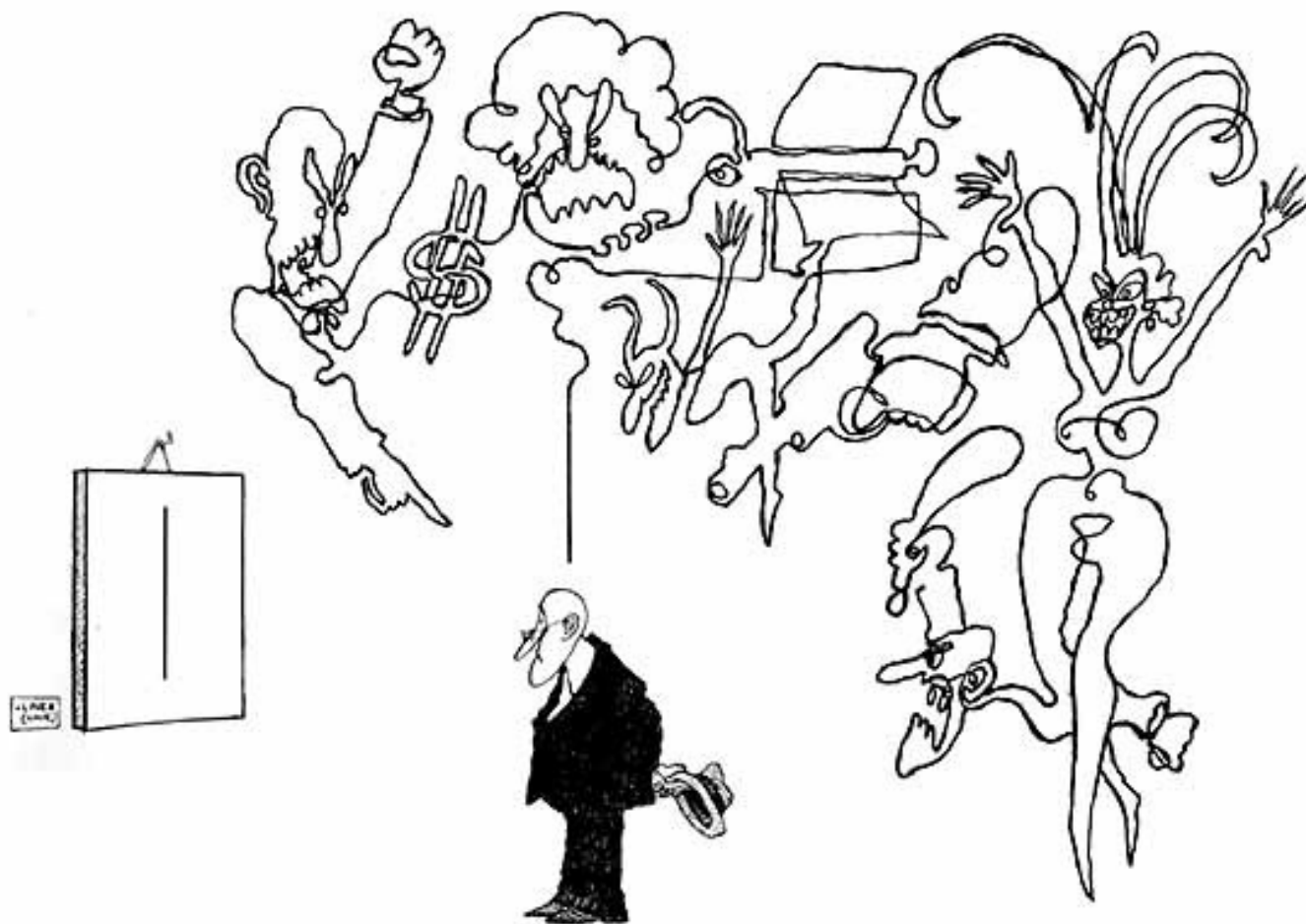
Lewinsohn et al. (2006) *Oikos* 113: 174-184

Resumen de patrones estructurales

- Pocas interacciones potenciales ocurren
- Desbalance entre número de plantas y animales
- Muchas especies con pocas interacciones
- Anidamiento
- Muchas interacciones débiles, pocas fuertes
- Asimetría en número y fuerza de interacciones
- Compartimentalización

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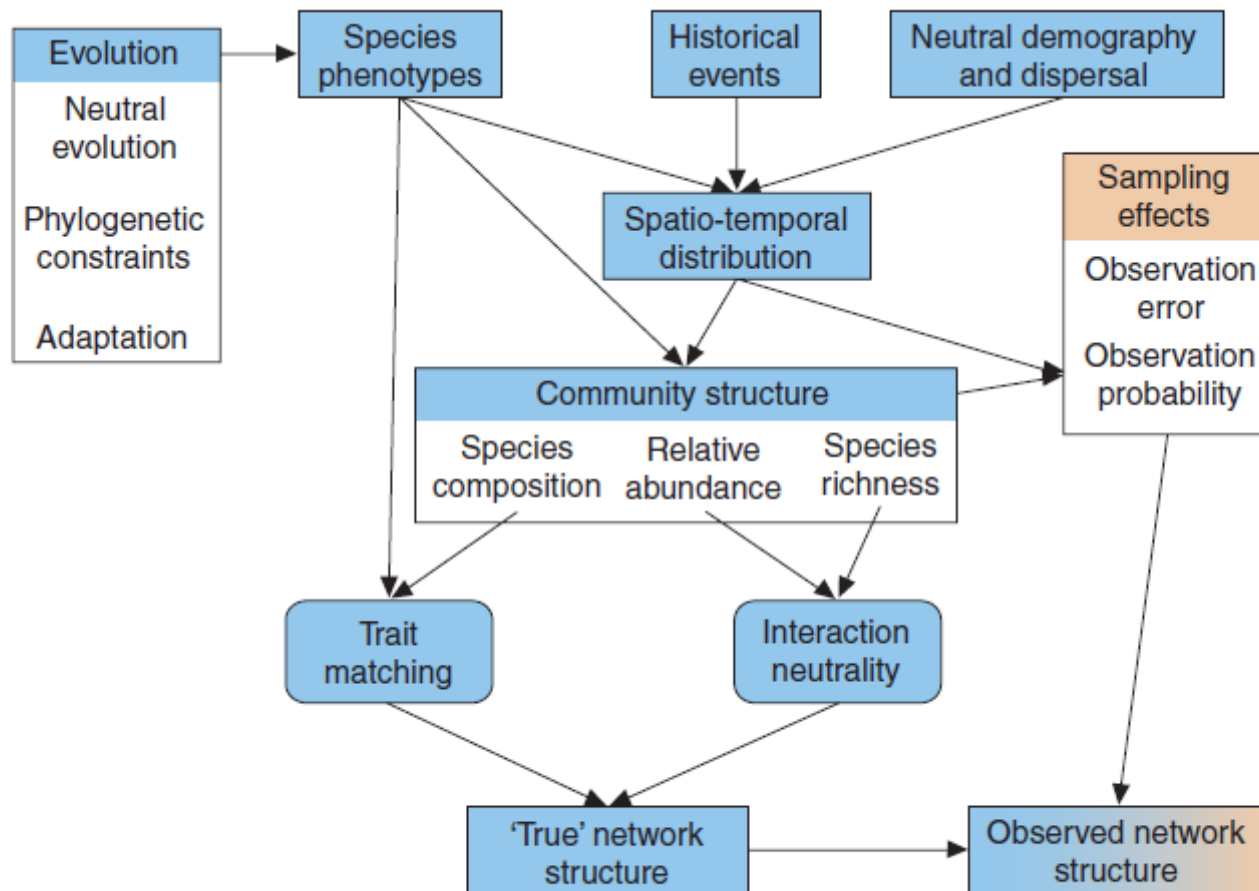
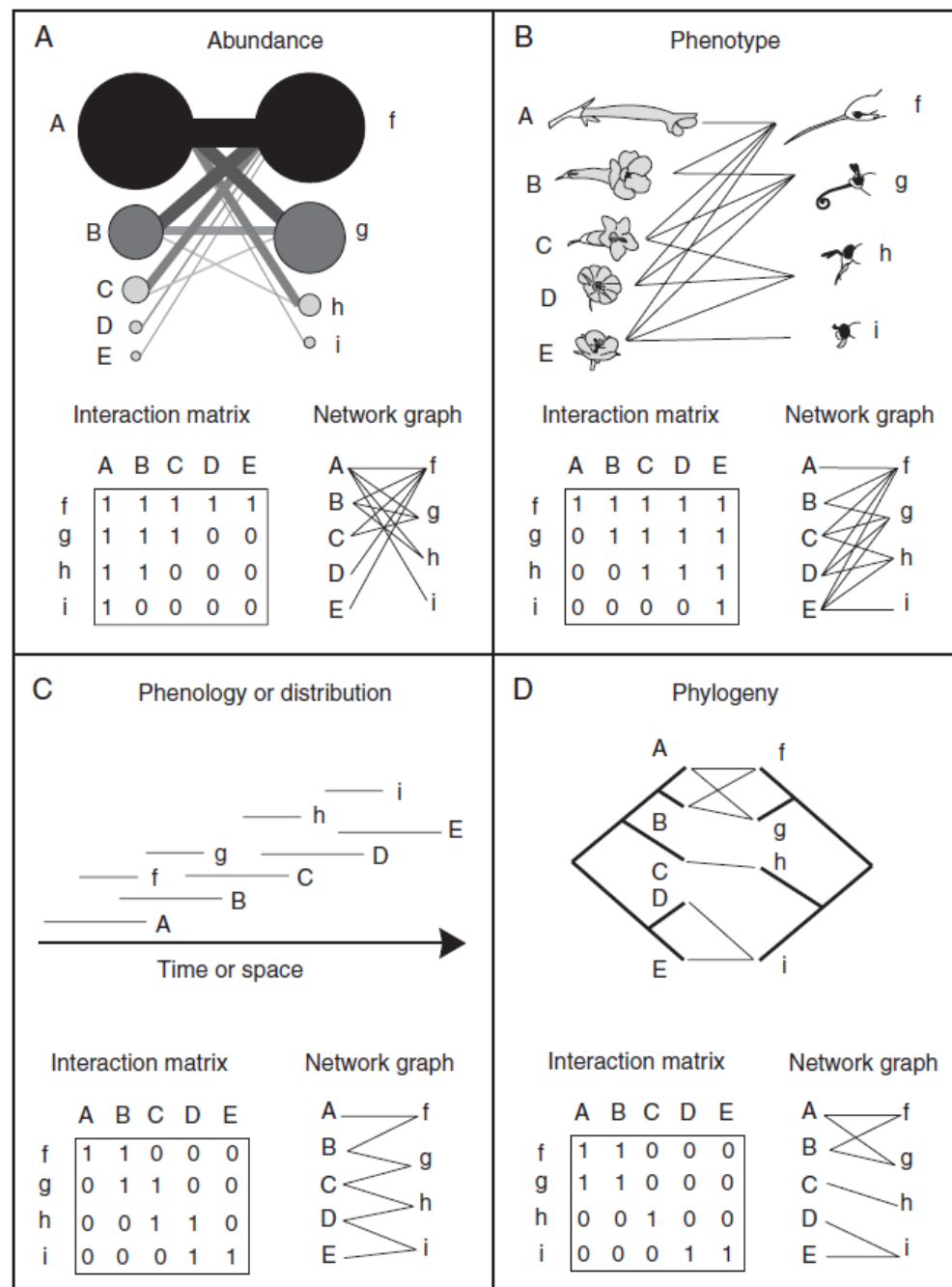
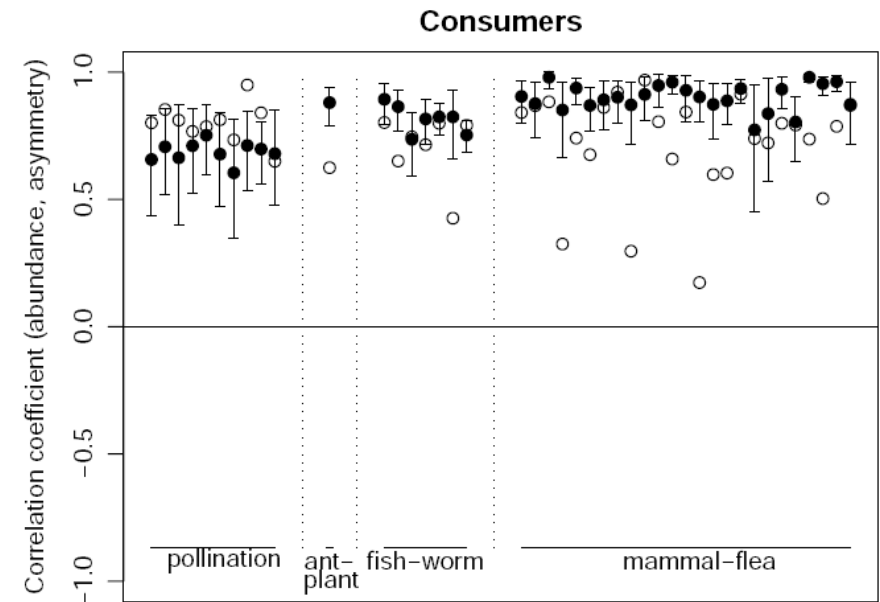
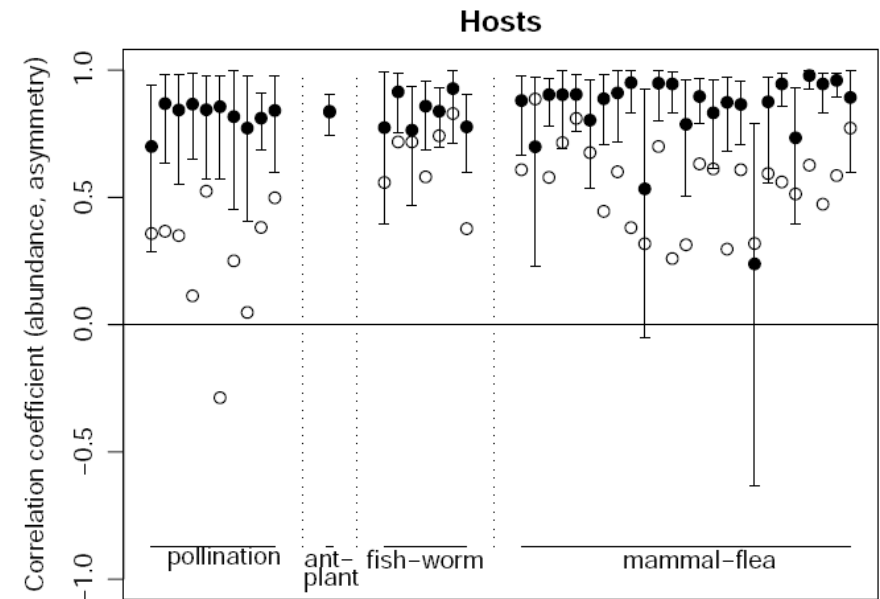
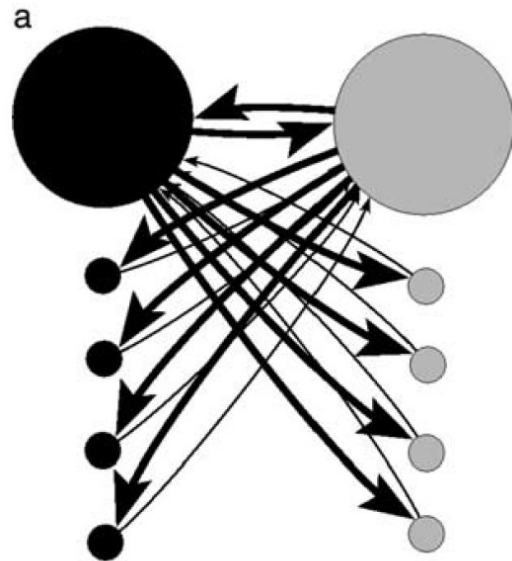


FIG. 1. Causal model of potential determinants of network structure.



Abundancia...



Vázquez et al. (2007) *Oikos* 116: 1120-1127

Tiempo...

Table 1 Values for properties of the plant–pollinator networks

	1983	1984	1985	1986	Total
<i>C</i>	2.6	2.6	2.9	3.0	3.4
<i>N</i>	0.982	0.977	0.971	0.981	0.970

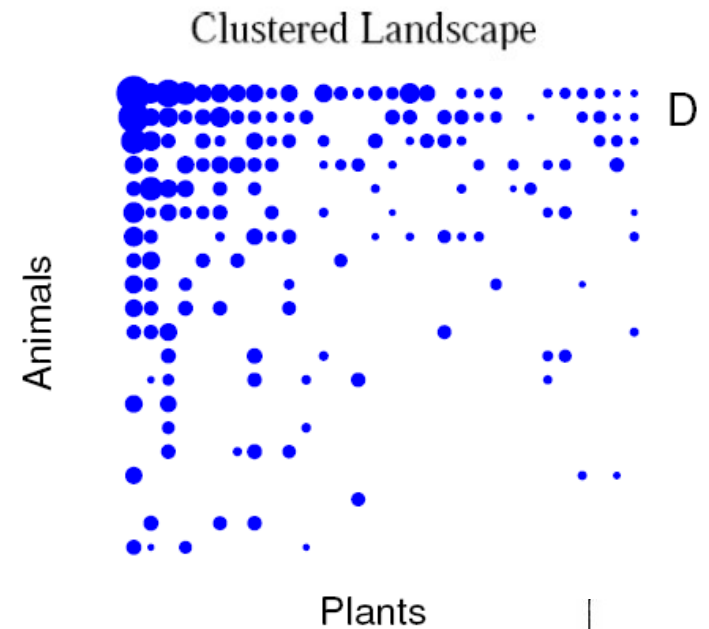
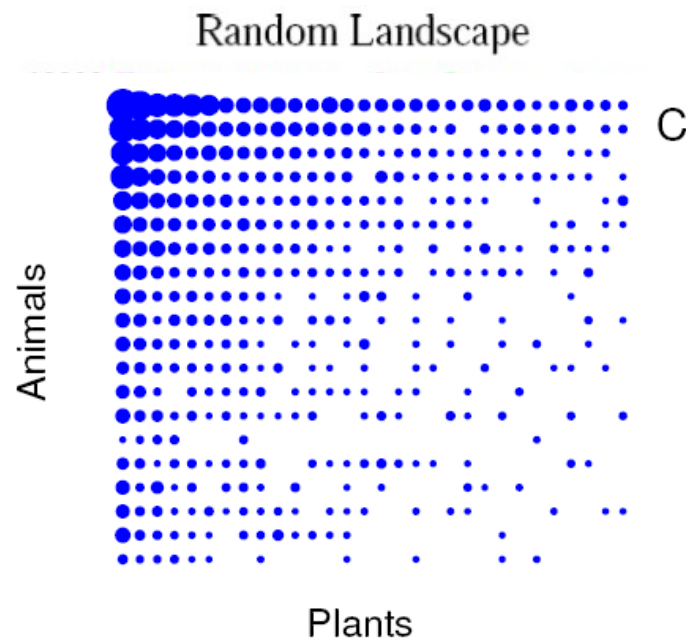
Table 2 Similarity between any pair of study years, given as number of common resources (plant species, insect species and interactions), and as Jaccard and modified Simpson indices

	1983 and 1984	1984 and 1985	1985 and 1986	1983 and 1985	1984 and 1986	1983 and 1986
<i>Number of species/interactions observed in both years</i>						
Plants	88	106	95	90	91	80
Insects	207	238	224	230	193	183
Interactions	282	407	355	331	288	246
Interactions of core species	223	290	276	254	248	221
<i>Number of interactions 'lost' between years, i.e. observed only in one over two years</i>						
Total number of interactions						
observed only in one year	1292	1665	1717	1697	1348	1314
Interactions lost among species present in both years	383 (29.6%)	603 (36.3%)	495 (28.8%)	510 (30.1%)	363 (26.9%)	289 (22.0%)
Interactions between a species present in both years and a partner species present in one year	687 (53.2%)	890 (53.4%)	919 (53.6%)	908 (53.5%)	694 (51.5%)	731 (55.6%)
Interactions between species that are present in only one year	222 (17.2%)	172 (10.3%)	303 (17.6%)	279 (16.4%)	291 (21.6%)	294 (22.4%)

Petanidou et al. (2007) Ecol. Lett. 11: 564–575



Espacio



Morales & Vázquez (2008) Oikos 117: 1362-1370

Correspondencia fenotípica

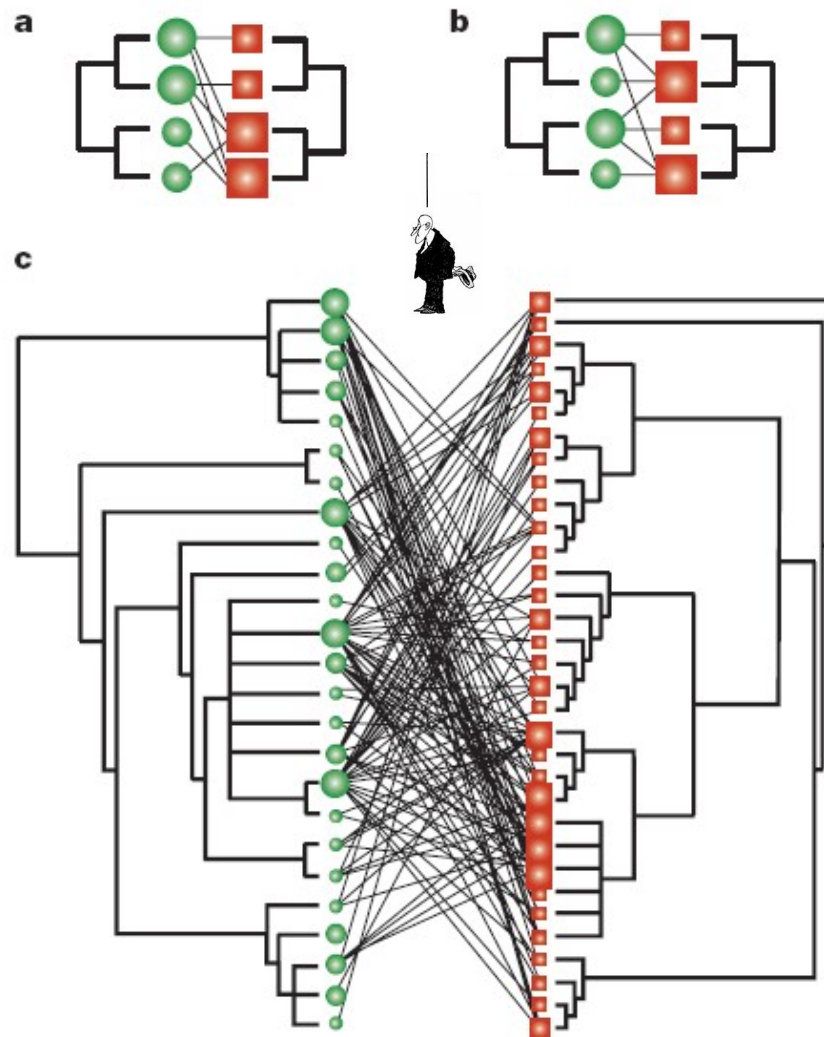
Table 3 Relationship between observed and random n (number of interaction partners) and observed and random m values (mean generalization level of interaction partners) for plants and flower visitors

Model	Explanation	Plants		Flower visitors	
		n_{vis}	m_{vis}	n_{pla}	m_{pla}
a	Equal probability, no size thresholds	-0.009 (0.260)	0.008 (0.254)	-0.002 (0.242)	-0.007 (0.259)
b	Nectar-holder depth threshold	0.402 (0.038)*	0.399 (0.051)	0.199 (0.073)	0.295 (0.003)**
c	Proportional visitor abundance	0.584 (0.003)**	-0.027 (0.314)	0.657 (<0.001)**	0.051 (0.234)
d	Visitor abundance, nectar holder depth	0.551 (0.004)**	0.479 (0.018)*	0.632 (<0.001)**	0.352 (0.009)**



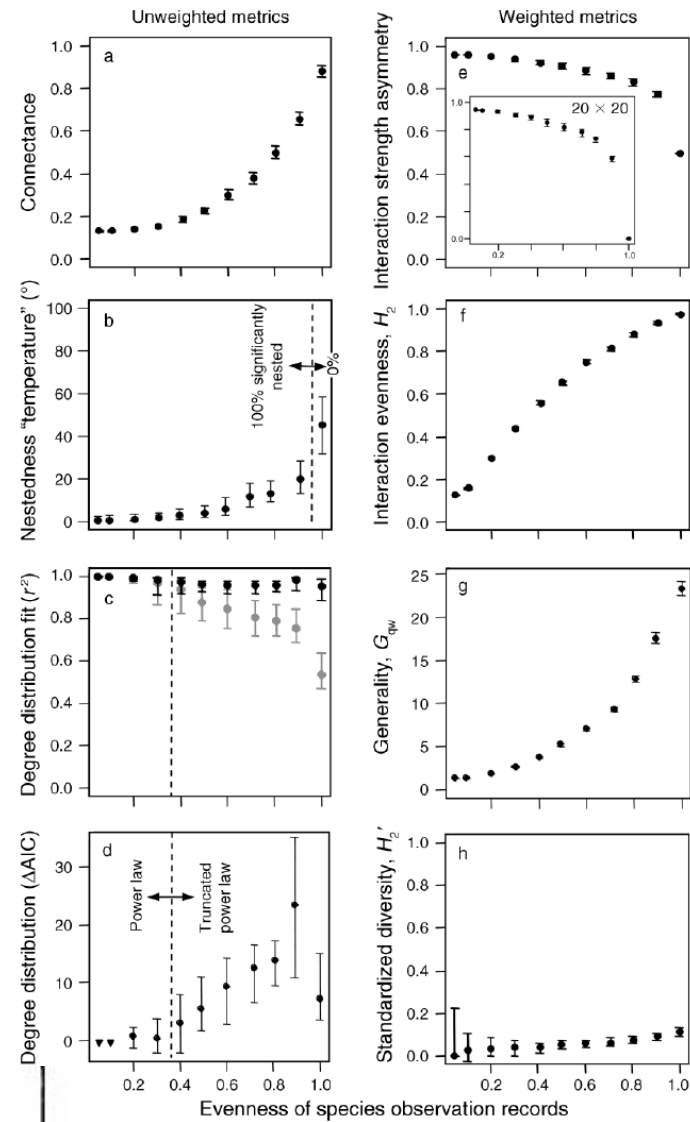
Stang et al. (2007) *Oecol.* 151: 442-453

Filogenia



Rezende et al. (2007) Nature 448: 925-928

Muestreo



Blüthgen et al. (2008) Ecology 89: 3387-3399

Poniendo todo junto...

$$\mathbf{Y} = f(\mathbf{N}, \mathbf{S}, \mathbf{T}, \mathbf{P}, \mathbf{K}, \mathbf{E})$$

Y: Matriz de interacción que queremos predecir

N, S, T, P, K and E: Matrices de probabilidad de interacción definidas por la abundancia, superposición espacial y temporal, relaciones filogenéticas, correspondencia fenotípica y efectos de muestreo

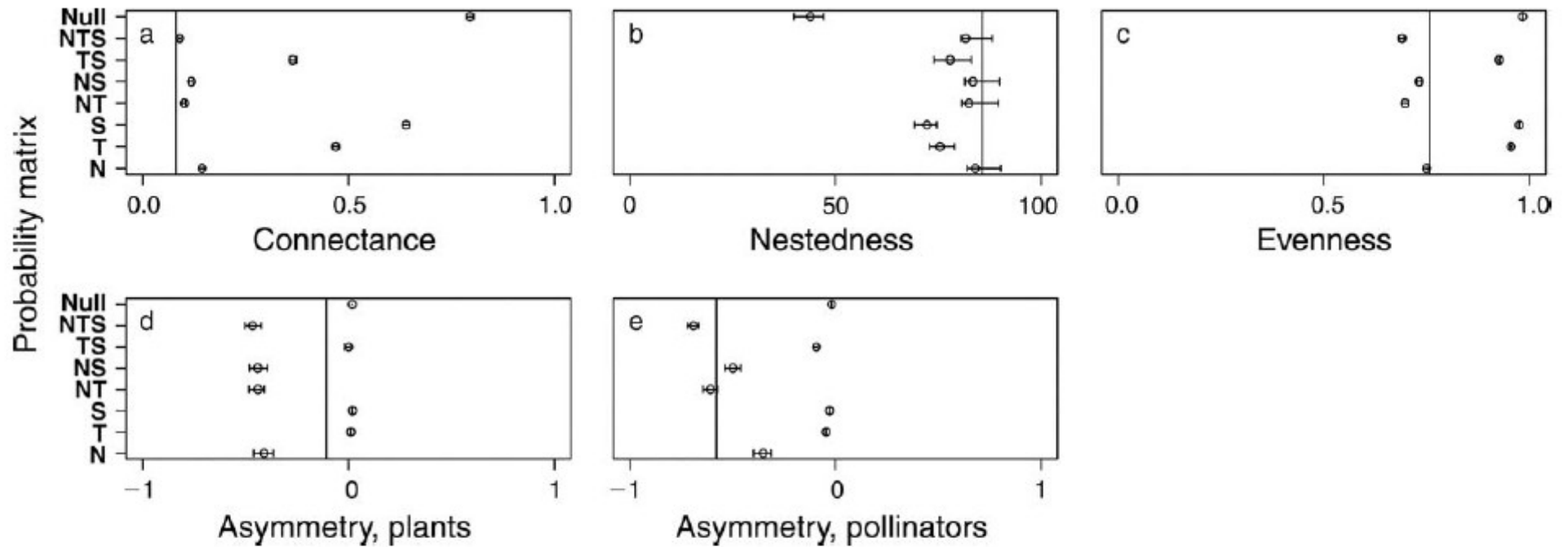
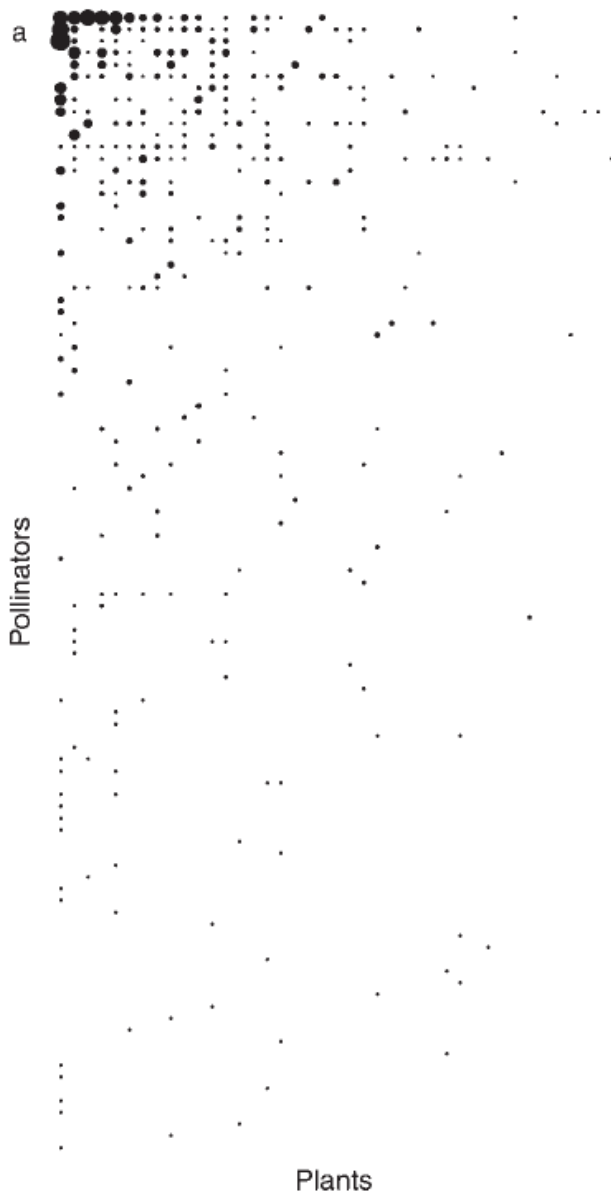
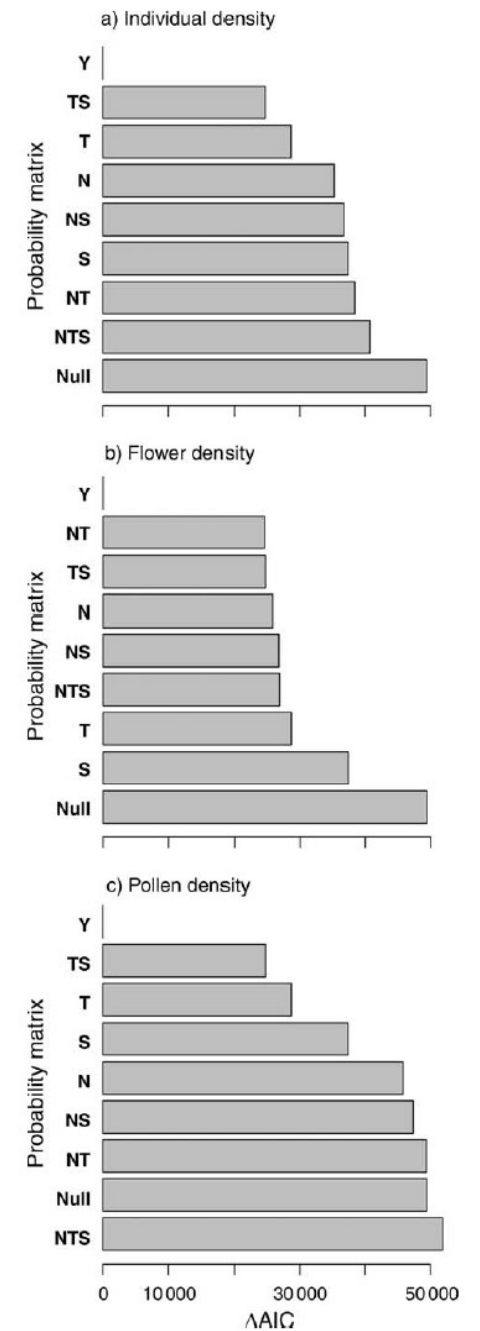
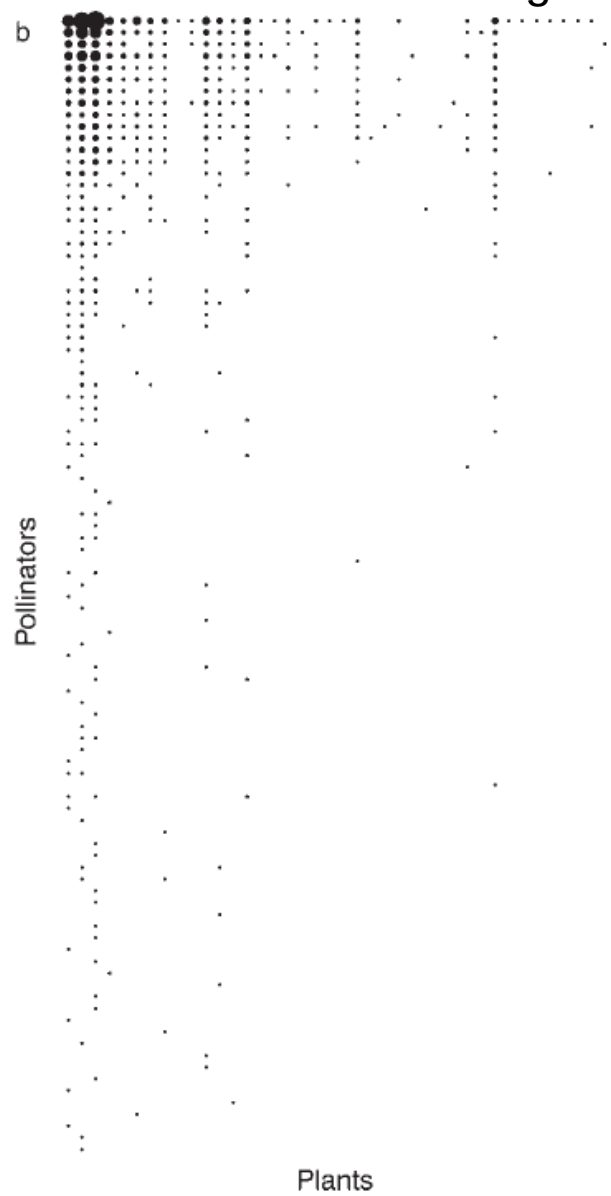


FIG. 2. Comparison between aggregate network statistics observed in the Villavicencio network (Monte Desert at Villavicencio Nature Reserve, Mendoza, Argentina) and those predicted by the probability matrices. In each panel, the vertical line represents the observed value of an aggregate statistic, and the circles represent the value of the statistic expected from each probability matrix, with error bars indicating 95% confidence intervals. Results are shown for the seven probability matrices resulting from all possible combinations of abundance (N), temporal overlap (T), and spatial overlap (S), and for the null probability matrix with homogeneous interaction probabilities across all pairwise interactions (Null).

Matriz observada



Matriz predecida por abundância e fenologia





Resumen de mecanismos

- Múltiples mecanismos contribuyen a generar la estructura observada de las redes de interacciones mutualistas
- Es importante considerar la abundancia y la distribución espacio-temporal
- El fenotipo impone restricciones importantes
- Los efectos de muestreo también tienen el potencial de influir sobre la estructura observada